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Research Article

Dispersal capacity as assessed by distance-decay relationships is lower for aquatic shredder insects than aquatic non-shredder insects in a Neotropical river network

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Abstract

Aquatic shredder insect diversity declines latitudinally toward the equator, contrary to the general latitudinal biodiversity gradient. Shredder diversity along tropical elevational gradients mimics this shredder latitudinal pattern. One of the hypotheses proposed to explain this pattern of diversity is that dispersal capacity drives variation in shredder assemblages given their low dispersal capacity in tropical streams. Additionally, tropical shredders probably have lower dispersal capacity than the rest of tropical aquatic insects, which have lower dispersal capacities than their counterparts in temperate areas. We tested this hypothesis in an elevational gradient of more than 2000 m in 16 reaches of streams distributed in the Usumacinta, Cahabon, and Polochic river watersheds. We quantitatively sampled aquatic insects and measured 12 environmental variables. We found a regional pool of 118 taxa, with 13 taxa classified as shredders, and 2 taxa of predator-shredders. Contrary to expectations, shredder rarefied richness decreased with increasing elevation, which suggests that dispersal capacity did not change with elevation. Assemblage similarity decreased with increasing distance between reaches due to low capacity to fly long distances. This relationship had a smaller slope when using the shortest spatial distances between pairs of reaches due to potential lateral scatter by flying adults. In sum, the results support the hypothesis that dispersal capacity drove aquatic shredder assemblage structure in these 16 tropical streams.

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Resumen

La diversidad de los insectos acuáticos fragmentadores de hojas declina latitudinalmente hacia el ecuador, contrario al gradiente latitudinal general de biodiversidad. La diversidad de este grupo a lo largo de gradientes de elevación tropicales tiene un patrón similar al patrón latitudinal de diversidad. Una de las hipótesis propuestas para explicar este patrón de diversidad de los insectos fragmentadores es que los insectos acuáticos fragmentadores tienen una capacidad de dispersión menor en zonas tropicales, menor incluso que el resto de insectos acuáticos tropicales que tienen capacidades de dispersión menores que sus contrapartes en áreas templadas. Pusimos a prueba esta hipótesis en un gradiente de elevación de más de 2000 m en 16 secciones de arroyos distribuidas en las cuencas de los ríos Usumacinta, Cahabón y Polochic. Hicimos colectas cuantitativas de insectos acuáticos y mediciones de 12 variables ambientales, simultáneamente. Encontramos 118 taxa entre todos los sitios, de los cuales 13 taxa

eran fragmentadores de hojarasca y 2 taxa depredador-fragmentador. Contrario a lo esperado, la riqueza, ponderada por la abundancia, de insectos fragmentadores disminuyó con la elevación, lo que sugiere que la capacidad de dispersión no cambia con la elevación. La similitud de los ensambles de fragmentadores disminuyó con el aumento de la distancia entre sitios debido a la baja capacidad de volar largas distancias. Esta relación tuvo una pendiente menor al usar la distancia más corta entre sitios debido a la potencial dispersión lateral por adultos voladores. Por lo tanto, los resultados dan soporte a la hipótesis de que la capacidad de dispersión controla el proceso de ensamblaje de insectos fragmentadores en estos 16 arroyos tropicales.

Key words: Bayesian linear models, Central America, dendritic network structure, freshwater insect assemblages, Guatemala

Palabras clave: América Central, Ensambles de insectos acuáticos, Guatemala, Modelos lineares bayesianos, Redes dendríticas

Introduction

A goal in ecology is to understand the mechanisms driving species assemblage structure in space and time (Hubbell 2001; Soberón and Peterson 2005). Assemblage structure drivers divide into two general groups, niche-based (Losos et al. 1998; Peterson et al. 1999) and dispersal-based mechanisms (MacArthur and Wilson 1967; Hubbell 2001; Thompson and Townsend 2006). Niche-based mechanisms suggest species with similar traits share a like environment, resulting in the resemblance of species assemblages decreasing with increasing environmental dissimilarity between sites (Peterson et al. 1999; Kluge and Kessler 2011; Montaño-Centellas et al. 2021). In dispersal-based mechanisms, species assemblage structure is driven by species dispersal capacity and spatial distance between sites, resulting in the similarity of species assemblages decreasing with increasing distance between sites, accompanied by variation in the strength of the relationship between assemblage similarity and environmental similarity (Brown and Swan 2010; Ge et al. 2023). The inherent hierarchical structure of stream networks makes it possible to contrast the influence of each of these two groups of mechanisms on the structuring of aquatic insect assemblages (Grant et al. 2007; Brown and Swan 2010; Saito et al. 2015).

Aquatic insects disperse among streams in three major potential ways: a) flying along stream corridors as adults, b) flying overland as adults, and c) drifting within streams as adults and larvae (Brown and Swan 2010; Lancaster and Downes 2013). Under a niche theory framework, flying along stream corridors is the major way to colonize headwaters from main channels (Thompson and Townsend 2006; Grant et al. 2007; Brown and Swan 2010). Therefore, an expectation is that assemblage similarity decreases with lower similarity in ecological conditions, independently of the spatial distance between headwaters (Brown and Swan 2010). One assumption for this expectation to be true is that organisms do not move among headwaters by flight overland because riparian forest is a barrier for dispersal activities. However, riparian forest might not be a complete barrier for overland flying between headwaters (Macneale et al. 2005). Therefore, if flying overland occurs between headwaters, assemblage similarity decreases with increased spatial distance among headwaters.

Dispersal capacities drove aquatic insect assemblage structures across large distances (i.e., >10 km) between headwaters streams in both Finland and New Zealand (Thompson and Townsend 2006; Mykrä et al. 2007). Because dispersal capacities vary among species, assemblage similarity decays with spatial distance between streams for species with low or medium dispersal capacities, with a steeper decay for the former. Strong dispersal overrides any relationship between assemblage similarity and spatial distance.

Aquatic insects are classified into six functional feeding groups (FFG) according to the predominant feeding strategy used to obtain food (i.e. shredder, collector-gatherer, collector-filter, piercer, scrapper, and predator; Cummins 1973). It is important to point out that insects from different FFGs can feed on similar food resources, such as diatoms, fungi, or animal tissue (e.g. García et al. 2016; Rosas et al. 2020), but they differ in the strategy to get that food (Cummins and Klug 1979). Some aquatic insect orders are classified almost entirely within an FFG, such as Odonata which are predominantly predators (Cummins et al. 2005; Ramírez and Gutiérrez-Fonseca 2014). While other orders of aquatic insects present two or more FFG states, such as Diptera, Coleoptera, and Trichoptera, where shredder, collector-filterer, predators, and scrapers are FFG that can be found (Cummins et al. 2005; Merritt et al. 2008). Feeding activities of aquatic shredder insects (i.e. breakdown leaf litter into smaller pieces) drive leaf litter decomposition to fine organic matter, and therefore they enable availability food for other aquatic species. Aquatic shredders consume up to 64% of stream leaf litter (Graça et al. 2015), and therefore can greatly reduce leaf litter standings stocks and downstream organic matter transport (Wallace and Webster 1996). Aquatic shredder insects occupy a central link in the food web between leaf litter (which is often the dominant source of organic matter to a forested stream) and predatory animals such as fishes and amphibians. Thus any processes that control aquatic shredder insect diversity in streams indirectly affect ecosystem functions of organic matter cycling and predator abundance.

Aquatic shredder insect assemblages have predominantly low α-diversity in tropical forest headwaters relative to temperate ones, despite γ-diversity of aquatic shredder insects in corresponding tropical regions is as high as in temperate regions (Boyero et al. 2015). This pattern is recurrent in aquatic shredder insects across tropical regions while non-shredder insects have higher α-diversity (Yule et al. 2009; Boyero et al. 2012). A hypothesis is that tropical shredders have lower dispersal capabilities than shredders at temperate streams (Boyero et al. 2015). Also, dispersal capabilities of tropical shredders should be lower than non-shredder insects given that tropical aquatic insects generally have lower dispersal capabilities relative to temperate ones (Polato et al. 2018). Variation in dispersal capacity was related to the strength of the relationship between assemblage similarity and the spatial distance between sites in aquatic insect assemblages of Brazil (Saito et al. 2015). Despite the evidence that dispersal capacity influences aquatic insect assemblage structure, we do not know how much dispersal capacity drives variation in tropical aquatic shredder assemblages, and thus determines patterns of low diversity in tropical streams.

We tested how dispersal capacity drove variation in aquatic shredder and non-shredder insect assemblages across 16 reaches of Neotropical headwaters streams in northern Central America. First, we tested the assumption that shredder richness increased with increasing elevation, and the assumption

that environmental dissimilarity increased with increasing spatial distances between pairs of reaches because there is a wide environmental gradient among 16 reaches. Second, there are two expected predictions that follow if dispersal limitation is driving assemblage structures (Brown and Swan 2010), 1) assemblage similarity decreases with increasing distance between pairs of reaches (i.e., Distance-decay relationship, DDR), 2) no relationship should exist between assemblage similarity and environmental dissimilarity between pairs of reaches. If shredders have a lower dispersal capability than non-shredders, then we expected that non-shredder assemblage similarity should decrease with increasing spatial distance at a slower rate than shredder assemblage. Third, given that dispersal can occur by adults flying overland (Brown and Swan 2010; Lancaster and Downes 2013), we expected a weaker relationship between shredder assemblage similarity and spatial distance between pairs of sites than the relationship between shredder assemblage similarity and shortest watercourse distance between pairs of sites (i.e., in-network distance). An alternative hypothesis to dispersal limitation as a driver of assemblage structure is that environmental factors drive variation in aquatic insect assemblages (Brown and Swan 2010). If that was the case, we expected 1) no relationship between assemblage similarity and spatial distance between pairs of reaches, and 2) a strong relationship between assemblage similarity and environmental dissimilarity between pairs of reaches.

Methods

Study site

We studied Salinas, Cahabon, and Polochic watersheds, draining 17371 km^2 from the central highlands in Guatemala to the northern lowlands (Fig. 1). The Salinas River watershed is the upper part of the Usumacinta River basin, one of the largest watersheds between the Isthmus of Tehuantepec and the Darien Strait (Hudson et al. 2005). The Cahabon and Polochic watersheds are adjacent to the Salinas River, Cahabon joins to the Polochic watershed before flowing into Izabal Lake, a lake that drains into the Caribbean Sea of northern Central America (Gall 1976, 1978; Elías et al. 2022). These watersheds span an elevational gradient from sea level to 3800 m asl, encompassing heterogeneity in climate, vegetation, and geology (MAGA and CATIE-ESPREDE 2001; Meave et al. 2021). Annual mean temperature ranges from 6 to 26C. Annual mean precipitation ranges from 700 mm in the drier area to 4000 mm on the most humid area of the watersheds. The precipitation pattern generates two general seasons throughout the year, a) a rainy season from June to October, and b) a dry season from November to May. Variation in temperature and precipitation is reflected on dominant terrestrial vegetation ecosystems through the watersheds (Meave et al. 2021).

Between June 2017 and March 2020, we conducted fieldwork in 16 stream reaches distributed along an elevation gradient of more than 2,000 m (Fig. 1, Table 1). The lowest site, Parque Nacional Laguna Lachuá (hereafter, Lachuá), is dominated by tree species of the genera *Terminalia* and *Vochysia*, which correspond to Tall Evergreen Rainforest (Selva Alta Perennifolia) (Rzedowski 2005; García 2006). Broadleaf montane forest characterizes vegetation in Sacmoc,

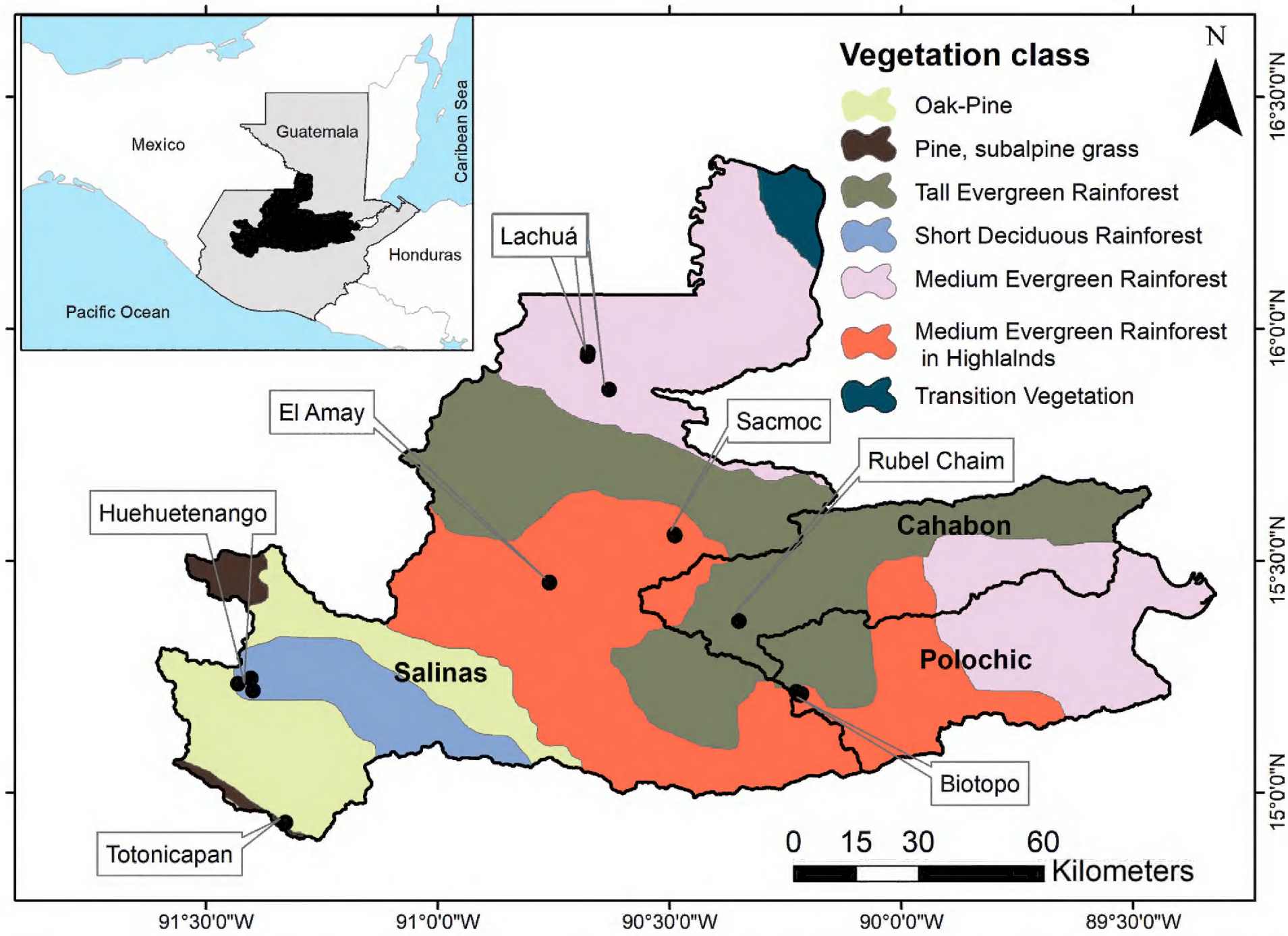

Figure 1. The 16 studied streams were located in distinctive vegetation classes within Salinas, Cahabon, and Polochic watersheds. Lachuá stands for Parque National Laguna Lachuá, a national park protecting a rainforest area. Biotopo stands for Biotopo Universitario "Mario Dary Rivera" para la Conservación del Quetzal, a national protected area of cloud forest that is administrated by the University of San Carlos of Guatemala. Totonicapan stands for Parque Regional Altos de San Miguel Totonicapán, a communal protected area of pine and oak forest. Sacmoc, El Amay, and Rubel Chaim are farms non-officially designated as protected areas by their owners. Streams in Huehuetenango were on the borders of farms and small villages, presented transitional evergreen forest between lowland rainforest and highland pine and oak forest. Vegetation class according to Méndez (2008).

El Amay, and Rubel Chaim sites, in the middle of the elevational gradient. Biotopo "Mario Dary Rivera" para la Conservación del Quetzal (hereafter, Biotopo) is a protected area of cloud forest (CECON 2007), and Parque Regional Altos de San Miguel Totonicapan (hereafter, Totonicapan) is a pine-oak forest (Albacete and Espinoza 2002; Cleary 2010). The study reaches selected were within protected natural areas with low human alterations to avoid changes in the diversity of aquatic insect assemblages due to anthropogenic stressors (Heino et al. 2003). Specifically, we looked for reaches with native vegetation within the catchment and riparian areas (i.e., natural riparian vegetation, and more than 85% of forest on whole catchment area), and without modifications to the stream channel. Canopy cover was less than 60% at Huehuetenango streams, it was a dry area of the Salinas River catchment with extensive cattle farms. All stream reaches were headwaters. Euclidean distances between pairs of sites were as short as 38 m, and as long as 132 km (Suppl. material 1: table S1). Distances over the river network were between 20 m to more than 382 km (Suppl. material 1: table S1).

Table 1. Site data for streams sampled, including average stream depth (*z*), average stream width (*w*), water velocity (*v*), discharge (*Q*), average of water temperature (T) followed by minimum and maximum within parenthesis, average of dissolved oxygen (DO) followed by minimum and maximum within parenthesis, electrical conductivity (EC), average of nitrate (NO^-_3–N), ammonium (NH^+_4–N), and soluble reactive phosphorous (SRP). *z*, *w*, *v*, and discharge are at baseflow. Lachuá stands for Parque Nacional Laguna Lachuá, a national park protecting a rainforest area. Biotopo stands for Biotopo Universitario "Mario Dary Rivera" para la Conservación del Quetzal, a national protected area of cloud forest that it is administrated by the University of San Carlos of Guatemala, Totonicapan stands for Parque Regional Altos de San Miguel Totonicapan, a communal protected area of pine and oak forest. Sacmoc, El Amay, and Rubel Chaim are farms non-officially designated as protected areas by their owners. Streams in Huehuetenango on the borders of farms and small villages, presented transitional evergreen forest between lowland rainforest and highland pine and oak forest.

Site	Stream	Latitude, Longitude	Elevation	Canopy Cover	*z*	*w*	*v*	*Q*	T	DO	EC	pH	NO^-_3–N	NH^+_4–N	SRP
		(D.ddd°)	(m asl)	(%)	(cm)	(m)	(m s^{-1})	(m^3 s^{-1})	(°C)	(mg L^{-1})	(µS cm^{-1})		(ug L^{-1})	(ug L^{-1})	(ug L^{-1})
Lachuá	Kixpur	15.86787, -90.63034	156	94.33	42.55	6.72	0.26	0.730	23.2 (21.9, 24.0)	7.2 (6.4, 7.4)	290	NA	338.7	7.4	127
Lachuá	Machacas	15.94848, -90.67544	194	92.45	25.50	4.36	0.04	0.049	23.0 (22.3, 23.4)	6.3 (6.0, 6.5)	275	6.38	53.8	5.4	2.7
Lachuá	Caoba	15.94035, -90.67623	168	86.01	27.01	2.09	0.01	0.008	20.8 (18.8, 22.3)	7.3 (6.9, 8.6)	105	5.56	21.5	3.7	13
Sacmoc	Sacmoc-1	15.55314, -90.48849	464	88	4.50	6.33	0.28	0.079	21.0 (20.8, 21.3)	8.1 (7.9, 8.4)	2941	7.47	258.3	7.7	2.57
Sacmoc	Sacmoc-2	15.55561, -90.48902	404	30.4	25.00	19.60	NA	NA	NA	NA	2973	NA	300	20	173
El Amay	Amay-1	15.45171, -90.75925	1385	69.12	60.19	3.43	0.33	0.690	17.2 (17.1, 17.7)	7.7 (6.6, 7.9)	442	6.82	13	13	<0.001
El Amay	Amay-2	15.45154, -90.75895	1385	69.45	3.66	2.80	NA	NA	NA	NA	424	6.65	53	13	<0.001
Rubel Chaim	Mestela	15.36805, -90.35033	1436	77.18	34.25	9.43	0.19	0.620	16.2 (15.4, 16.9)	8.0 (7.6, 8.3)	409	NA	320.7	3.7	0.95
Huehuetenango	Caya	15.21812, -91.39980	1606	73.5	15.49	3.45	NA	NA	18.4 (16.3, 21.1)	6.5 (5.9, 7.5)	129	6.91	23.1	7.4	127
Huehuetenango	Xeteman	15.24502, -91.40240	1711	50	9.71	2.02	NA	NA	17.5 (14.7, 20.6)	4.1 (0.8, 7.1)	131	NA	4.6	3.8	179
Huehuetenango	Sachil	15.21870, -91.39857	1601	60	1.08	3.42	0.16	0.006	20.4 (15.3, 27.7)	6.3 (5.5, 7.3)	149	6.41	6.4	6	223
Biotopo	Hapaj	15.21574, -90.22646	1755	59.69	11.21	4.02	0.03	0.011	14.9 (13.8, 16.1)	8.1 (7.8, 8.3)	98	NA	378.3	5	12.2
Biotopo	Musgos	15.20866, -90.22074	1942	88.12	8.88	2.85	0.02	0.006	12.7 (11.7, 13.7)	7.9 (7.7, 8.1)	49	6.6	338.7	67.1	6.4
Biotopo	Biotopo-1	15.21065, -90.21607	1826	80.35	8.33	0.94	0.06	0.016	16.1 (15.5, 16.5)	8.0 (7.9, 8.1)	42	6.73	80.35	20	90
Biotopo	Biotopo-2	15.20865, -90.21608	1933	70.33	0.03	0.78	0.06	0.006	15.8 (15.3, 16.3)	7.5 (7.4, 7.6)	38	6.51	70.33	10	240
Totonicapan	Las Minas	14.93340, -91.32787	2720	85.25	8.66	1.09	0.07	0.007	10.7 (8.0, 13.2)	7.6 (7.3, 8.2)	54	6.56	131.5	9.7	19

Freshwater insects sampling

We worked at baseflow in the dry seasons from 2017 to 2020. We sampled each site on one occasion within this period of time. We quantitatively sampled benthic insects using a Surber net (250 µm mesh, and a frame area of 30×30 cm). We collected 6 Surber sub-samples within 100 m at each reach, moving from downstream to upstream to avoid disturbing the reach during sampling. We preserved half of the samples in 95% ethanol, and the second half in Kahle's solution for 72 h and then transferred to 95% ethanol. We identified every insect to the lowest taxonomic level possible (i.e., mostly genus) using the available taxonomic keys for the region (Merrit et al. 2008; Bueno-Soria 2011; Hamada et al. 2018), except some flies such as Chironomidae (Diptera) that we classified as Tanypodinae and non-Tanypodinae. We classified each taxon to functional feeding groups (FFG) following the literature (Cummins et al. 2005; Merritt et al. 2008; Ramírez and Gutiérrez-Fonseca 2014).

Site environmental characterization

At each study reach, we recorded 12 environmental variables to describe location, as well as chemical, and physical characteristics. Latitude, longitude, and elevation (m asl) were recorded. Average of stream wetted width (*w*) was calculated from ten locations at constant intervals through the study reach. We estimated stream discharge (*Q*) based on the slug-injection method using the NaCl tracer to change specific conductivity (Gordon et al. 2004; Day and Hall 2017). Water velocity (*v* in m min^{-1}) was estimated by dilution gauging of one kilogram of NaCl using an Onset HOBO conductivity logger, and converting the values to specific conductivity (e.g. Day and Hall 2017). We calculated the mean of electrical conductivity (EC) for 15 min every 3 s before adding NaCl tracer. Water temperature (T in °C) and dissolved oxygen (DO in mg L^{-1}) was recorded every 10 min for 3–30 days using a PME MiniDOT logger. Three water samples, previously filtered using glass fiber (GF/F) filters and frozen to be transported to USA, were used to quantify nitrate (NO^{-}_{3}–N), ammonium (NH^{+}_{4}–N), and soluble reactive phosphorus (SRP). All water samples, except those from Biotopo-1, Biotopo-2, Amay-1, and Amay-2, were processed at the Freshwater Research Lab at Flathead Lake Biological Station following standard protocols. NO^{-}_{3}–N was measured by the azo dye colorimetric method (EPA Methods 353.2). NH^{+}_{4}–N was measured by the indophenol colorimetric method (EPA 350.1). SRP was measured by the ascorbate acid colorimetric method (EPA 365.1). Water samples from Biotopo-1, Biotopo-2, Amay-1, and Amay-2 were processed in the field using a field colorimetry kit (Smart 2 LaMotte Industries). To estimate nutrient concentration of these water samples, we estimated NO^{-}_{3}–N by cadmium reduction colorimetry method, NH^{+}_{4}–N by salicylate colorimetry method, and SRP by ascorbate acid colorimetric method.

Data analysis

There was high variation in the total number of individual insects sampled across reaches (non-shredder: min = 10, max= 1866; shredder: min= 4, max=203). Thus, we rarefied observed richness by reach to minimum sampled

individuals per reach to account for the influence of sample size over observed richness (Colwell et al. 2012; Oksanen et al. 2022). Rarefactions were conducted using the "rarefy" function in the "vegan" package in R (Oksanen et al. 2022). We tested how rarefied richness (R) varied with elevation (m) by fitting the following linear model (Bürkner 2017; Gelman et al. 2020):

$$R \sim Poisson(e^{b_0+b_1 m}) \quad (1)$$

where b_0 and b_1 are parameters. We were interested in assessing the variation in the parameters given the state of shredder in the functional feeding group trait. There were two trait categories, shredder and non-shredder; we set as baseline the non-shredder state (b_0 and b_1), and the shredder state (β_s and α_s) as added variation over b_0 and b_1 such that:

$$R \sim Poisson(e^{b_0+\beta_s+(b_1+\alpha_s)m}) \quad (2)$$

We used as a weakly informative prior for $b_1 \sim N(0,3)$. We excluded site Amay-2 because it had just 2 shredder individuals.

We assessed how aquatic shredder insect dispersal capacity was related with aquatic non-shredder insect dispersal capacity by comparing the slopes of the linear relationship between assemblage similarity (A) and distance (D) between pairs of sites (i.e., distance-decay relationships, DDR) (Brown and Swan 2010):

$$A = b_0+b_1 D \quad (3)$$

We calculated A using the Bray-Curtis similarity index (Magurran and McGill 2011). We calculated D, in km, in two ways to consider potential overland and watercourse dispersal pathways (Brown and Swan 2010; Lancaster and Downes 2013; McCreadie and Bedwell 2014). First, we calculated D as the Euclidean distances (D_e) between pairs of reaches (shortest overland distance between two sites), based on their geographic coordinates. Second, we calculated D as in-network distances (shortest watercourse distance between two reaches, D_r). We calculated D_r between pairs of reaches within the same watershed. We estimated slope in equation 1 fitting a Bayesian linear model with a Zero-inflated Beta distribution given A had values between zero and one, but also including zero. As in equation 2, we set non-shredder state of the functional feeding group trait as a baseline (i.e., b_0 and b_1), and shredder state of the functional feeding group trait as variation (i.e., β_s and α_s) in parameters of the model (i.e., b_0 and b_1). Prior probability for b_1 was $b_1 \sim N$ (-0.07, 0.02), given the mean and confidence intervals for DDR slopes of aquatic macroinvertebrate assemblages for a global data set (Boyero et al. 2015).

We evaluated the relationship between environmental dissimilarity and assemblage similarity by substituting environmental dissimilarity (E) for D_e or D_r in the linear model of equation 3. We calculated E using the Euclidean distance for the 12 standardized environmental variables. We fit a Bayesian linear model with Zero-inflated Beta distribution too. As in equation 2, we set non-shredder condition as baseline (i.e., b_0 and b_1), and shredder condition as variation

(i.e., β_s and α_s) in parameters of the model (i.e., b_0 and b_1). We used as prior probabilities $b_1 \sim N$ (-0.06,0.05) given mean value and confidence interval reported of relationship between benthic macroinvertebrate assemblage similarity and environmental dissimilarity (Brown and Swan 2010).

We assessed the relationship between E and D_e fitting the linear model of equation 2, substituting E for A. We fit a Bayesian linear model with a Normal distribution. We used weakly informative priors $b_0 \sim N$ (0,10), and $b_1 \sim N$ (0,10).

We fit all models by simulating the posterior parameter distributions using the "brms" package in program R (Bürkner 2017; Core Team R 2017). We ran simulations to the posterior distributions on four Markov Chain Monte Carlo (MCMC). MCMC sampling of posteriors was performed in 1000 iterations by chain after burn-in. We visually checked chain convergence and the scale reduction factor, $\hat{R} < 1.1$, for all parameters.

Results

Most taxa were non-shredder (118) with 13 taxa classified as shredder functional feeding group (Suppl. material 1: table S2), and 2 taxa were predator-shredder. Shredder richness varied between 2 to 10 taxa by reach, while non-shredder richness varied between 8 to 50 taxa by reach. Predator groups had the largest sampled richness with 40 taxa, and the other 4 taxa were identified as collector-filter predators. Four taxa were classified as algae-piercers.

Contrary to expectation based on previous findings of positive relationship between richness and elevation (Camacho et al. 2009; Yule et al. 2009), rarefied richness, both shredder and non-shredder, did not vary with increasing elevation after weighting richness by the number of individuals collected by reach (Fig. 2). Low shredder richness could reflect low abundances e.g., Totonicapan reach with 8 individuals of shredders within 2 species. However, shredder abundance was not related to general low abundance in the Totonicapan reach given that non-shredders had a high sampled abundance (1546 individuals) relative to other reaches in El Amay or Biotopo sites (10 and 96 individuals, respectively).

Negative DDR slopes indicated potential dispersal dynamics driving assemblage structure of shredder and non-shredder assemblages (Fig. 3). Assemblage similarity, both shredder and non-shredder, decayed with increasing Euclidean distances at similar rate. Shredder assemblage similarity decayed with increasing in-network distances, while non-shredder assemblage similarity did not vary with increasing in-network distances. The DDR relationship was 1.6 times weaker for the shredder assemblage similarity and Euclidean distance relationship (i.e., Slope = -6.4×10^{-3}, C.I. = -9.6×10^{-3}) than for the shredder assemblage similarity and in-network distance relationship (i.e., Slope = -3.9×10^{-3}; C.I. = -5.4×10^{-3}), which suggests that adult shredder dispersed overland. Assemblage similarity, both shredder and non-shredder, did not vary with increasing environmental dissimilarity. There was a positive relationship between environmental dissimilarity and increasing Euclidean distances between pairs of reaches (Fig. 4), which supports dispersal dynamics as a driver of assemblage structure across study sites.

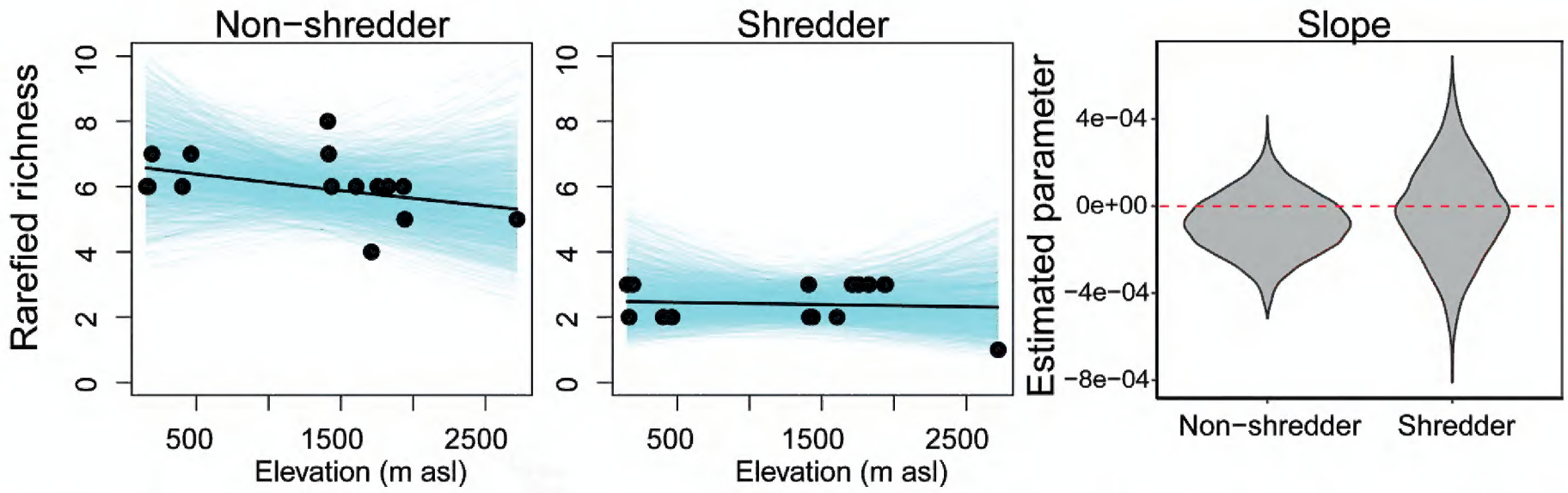

Figure 2. Rarefied richness, both shredder and non-shredder, did not vary with increasing elevation. Dots are rarefied richness for non-shredder and shredder of 15 reaches in an elevational gradient from 156 to 2720 m asl in northern Central America. Black solid lines are the mean fit Bayesian linear model between variables with a Poisson distribution. Blue faded lines are a 1000 possible lines from the Bayesian posterior distribution of the fitted model. Third panel shows a density plot of estimated values for slopes, dashed red line indicates the zero value.

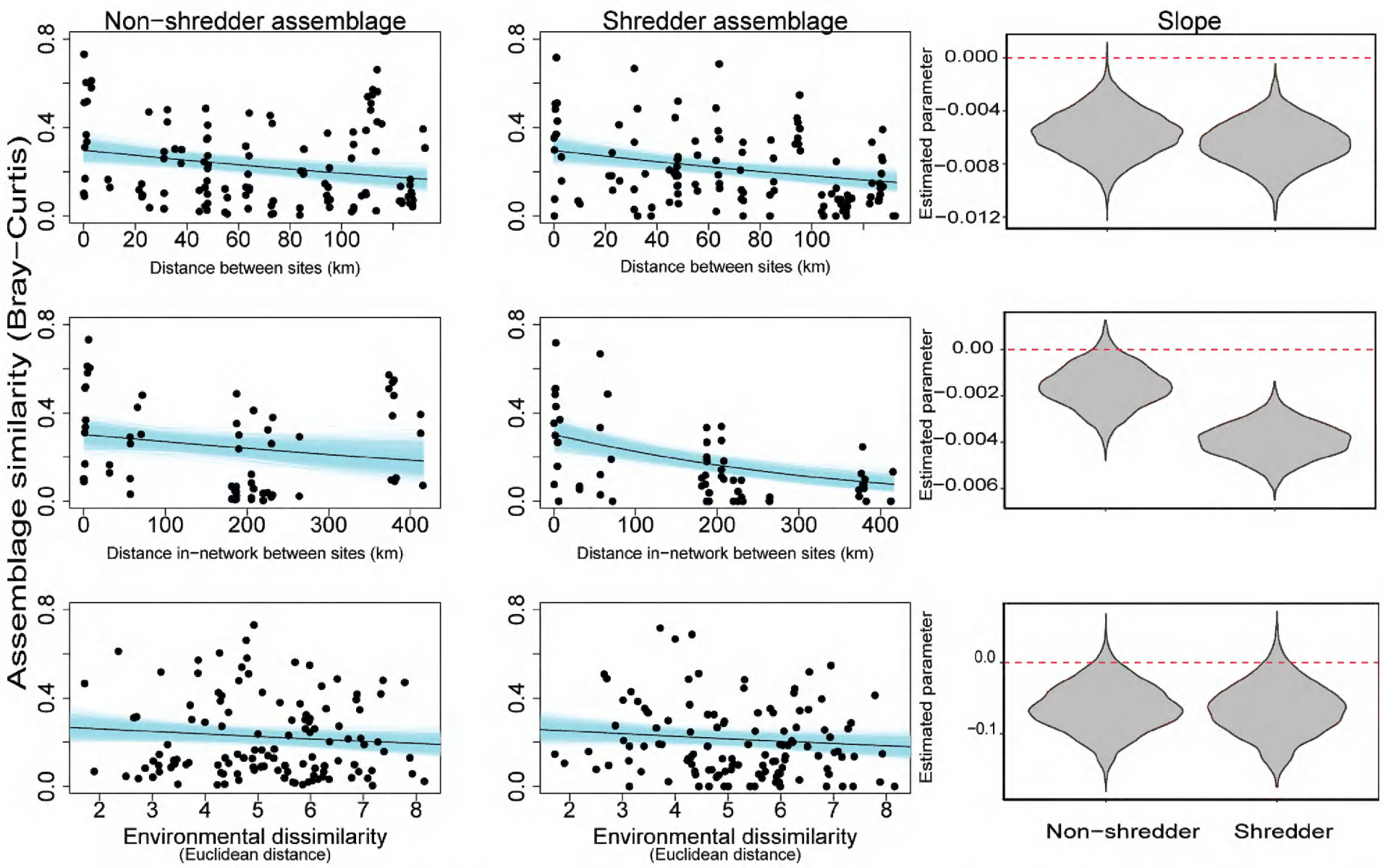

Figure 3. Relationships between assemblage similarity and distance show stronger strength of dispersal role on structuring aquatic shredder insect assemblages compared to aquatic non-shredder insect assemblages. Dots are assemblage similarity and distance between pairs of 16 reaches in an elevational gradient from 156 to 2720 m asl in northern Central America. Black solid lines are the mean fit Bayesian linear model between variables with a Zero-inflated Beta distribution. Blue faded lines are a 1000 possible lines from the Bayesian posterior distribution of the fitted model. Third column shows density plots of estimated values for slopes, dashed red line indicates the zero value.

Discussion

Distance-decay relationships (DDR) documented here indicate lower dispersal capacity for shredders than non-shredders along the river network. Aquatic insect richness did not vary with increasing elevation. Shredder state of the func-

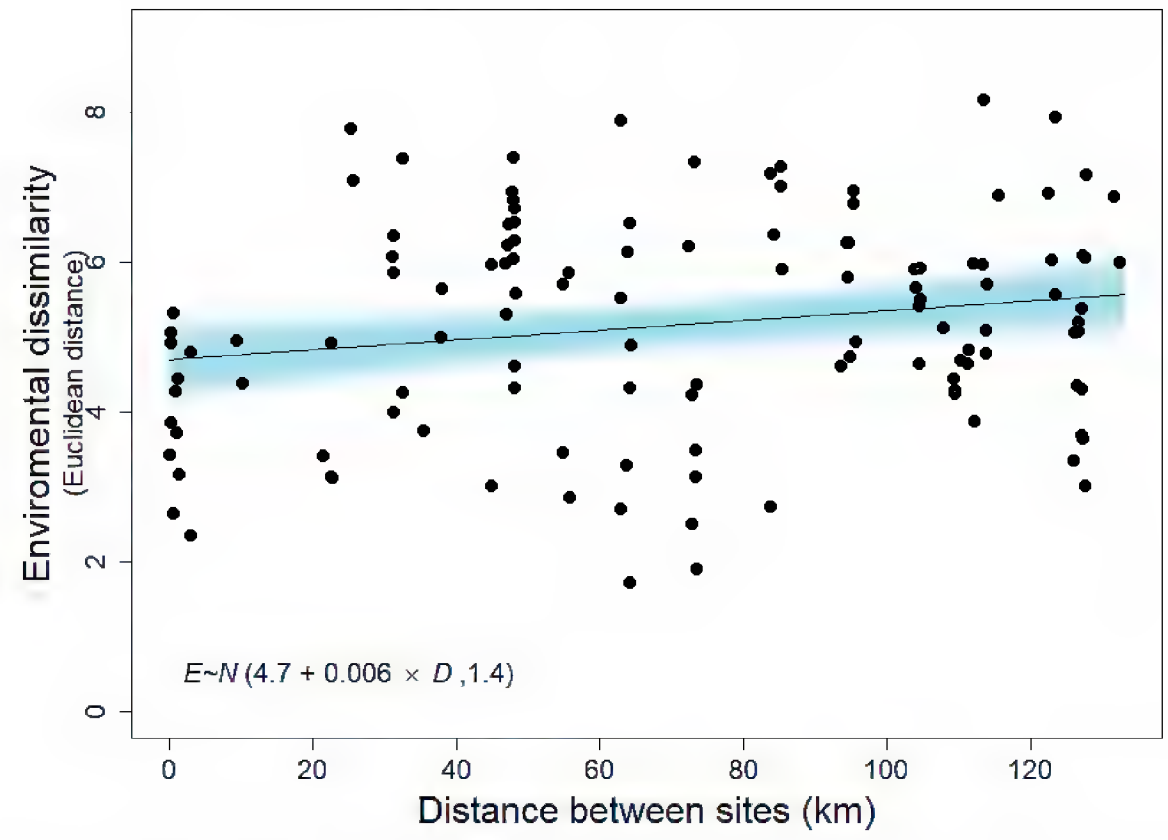

Figure 4. Positive relationship between environmental dissimilarity and spatial distance agrees with the predictions for an assemblage structure controlled by dispersal dynamics (Brown and Swan 2010). Dots are environmental dissimilarity and spatial distance between pairs of 16 reaches in an elevational gradient from 156 to 2720 m asl in northern Central America. Black solid lines are the mean fit Bayesian linear model between variables with Normal distribution. Blue faded lines are a 1000 possible lines from the Bayesian posterior distribution of the fitted model.

tional feeding group trait had no effect on DDR when using Euclidean distance, while it turned a DDR with a slope of zero into a DDR with a negative slope when in-network distance was used. Shredder DDR decayed 1.6 times faster with Euclidean distance between pairs of sites than with in-network distance between pairs of sites. Assemblage similarity, both shredder and non-shredder, did not change with environmental variation between pairs of reaches.

Patterns of shredder richness across elevation did not match expectation based in previous studied tropical elevational gradients; richness did not vary with increasing elevation. Previous findings have shown an increasing shredder richness with increasing elevation in the humid tropics of Australia and Malaysia (Camacho et al. 2009; Yule et al. 2009). One potential source of our contrasting result may be the use of rarefied richness because previous work did not weigh richness by abundance, despite the known influence of sample size on richness (Colwell et al. 2012). Lack of variation in shredder richness along elevational gradients has been observed in Kenya and Panama, even when richness was not weighed by abundance (Dobson et al. 2002; Camacho et al. 2009). A plausible explanation for the general low richness of shredders could be misassignment of taxa as shredders, in combination with low leaf litter availability in quantity and quality (Dobson et al. 2002). Here, misassignment was unlikely because the assignment to functional feeding groups was based on information specific for Neotropical taxa (Cummins et al. 2005; Ramírez and Gutiérrez-Fonseca 2014).

Species richness at a site is influenced by sample size (Colwell et al. 2012). Therefore, we cannot find more species than the number of individuals sampled at any site. Weighting richness by abundance (i.e. rarefied richness) can change where the peak of richness is in an elevational gradient, as it is observed

for richness for vegetation with a peak of richness at low elevations instead of mid-elevations (Ibanez et al. 2016). Given this, to ensure comparability, it is recommended that richness between localities be done by comparing rarefied richness (e.g. Griffiths et al. 2021).

Negative slopes of the relationship between shredder assemblage similarity and spatial distance suggest that shredder assemblage structure may be partially driven by dispersal dynamics (Brown and Swan 2010). Shredder assemblages had negative DDR slopes, which suggest that shredders had low to moderate dispersal capacity given that high dispersal capacity weakens or eliminates this relationship (Thompson and Townsend 2006; Ge et al. 2023), as in the case of non-shredder assemblages. Furthermore, a shallower DDR slope with Euclidean distance than with in-network distance suggests that lateral dispersal may control similarity among shredder assemblages (Brown and Swan 2010). One caveat is that we did not measure directly the distance that shredder species dispersed at the study sites. However, overland dispersal movement is a plausible explanation for the observed assemblage similarity between sites, as Euclidean distances between sites (e.g., 200 and 900 m) were shorter than distances over watercourses in the corresponding sites (e.g., 1.5 to 9 km). We know that aquatic insects can fly from 200 to 900 m overland and over watercourses (Macneale et al. 2005; Finn and Poff 2008). Additionally, estimated DDR slopes for shredders were 25 times smaller than slopes estimated for freshwater benthic macroinvertebrate assemblage similarity across 91 sites in North America (Brown and Swan 2010), suggesting detection of small effect size.

Assemblage similarity, for both shredders and non-shredders, did not change as a function of environmental dissimilarity between pairs of sites. This pattern in combination with the positive relationship between environmental dissimilarity and Euclidean distance between pairs of reaches suggests that local environmental factors did not drive assemblage structure (Brown and Swan 2010). These results contrast to previous findings in temperate zones where environmental factors and dispersal drove assemblage structure (Thompson and Townsend 2006; Mykrä et al. 2007; Brown and Swan 2010; Heino and Tolonen 2017). The positive relationship between environmental dissimilarity and Euclidean distance between sites, as expected, rules out the possibility that the studied environmental gradient was too small. Null relationships between assemblage similarity and environment have been previously reported for tropical aquatic insects with low dispersal capacity (Boyero et al. 2015; Saito et al. 2015). Altogether, these absences of relationships suggest that dispersal limitation, rather than environmental factors, was the main driver of species assembly structure.

Conclusions

This work supported the hypothesis that dispersal capacity drives shredder assemblage structure in Neotropical streams. We found evidence that aquatic shredder insects have lower dispersal capacity than aquatic non-shredder insects, and flying overland could be a pathway to connect assemblages between headwaters streams. To date, studies have focused on assessing environmental variables as drivers of aquatic insect assemblage structure (Heino et al. 2003; Heino and Tolonen 2017). However, there is accumulating evidence that neutral

processes such as dispersal control the assemblage structure (Thompson and Townsend 2006; Boyero et al. 2015; Saito et al. 2015). In the case of shredder assemblages, we assessed dispersal capacity as a driver of assemblages of a small number of reaches. Negative slopes of DDRs, together with the lack of relationship between assemblage similarity and environmental dissimilarity, suggest that dispersal limitations contribute to structuring shredder assemblages in these streams, despite the small number of sites studied. Therefore, future work should assess a) how far do aquatic shredder insects fly overland and over watercourses? and b) how much gene flow exists among shredder populations that are spatially close overland, but far in terms of stream network distance?

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: ROHJ, PG. Data curation: PG. Formal analysis: PG. Funding acquisition: ROHJ, PG. Investigation: PG. Methodology: PG, ROHJ. Project administration: PG. Resources: PG, ROHJ. Software: ROHJ, PG. Supervision: PG. Validation: PG. Visualization: PG. Writing - original draft: PG. Writing - review and editing: ROHJ, PG.

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Data availability

All data and r code is available at https://github.com/pavka17/Distance-decay-relationships.

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Supplementary material 1

Overland (km) and in-network (km) distances between sampling sites. Freshwater insect taxa and functional feeding groups

Authors: Pavel García, Robert O. Hall Jr

Data type: pdf

Explanation note: **table S1.** Overland (km) and in-network (km) distances between sampling sites. Overland distances are below the black diagonal line and in-network distances are above the diagonal line. Lachuá stands for Parque Nacional Laguna Lachuá, a national Park protecting a rainforest area. Biotopo stands for Biotopo Universitario "Mario Dary Rivera" para la Conservación del Quetzal, a national protected area of cloud forest that it is administrated by the University of San Carlos of Guatemala, Totonicapan stands for Parque Regional Altos de San Miguel Totonicapan, a communal protected area of pine and oak forest. Sacmoc, El Amay, and Rubel Chaim are farms non-officially designated as protected areas by their owners. Streams in Huehuetenango on the borders of farms and small villages, presented transitional evergreen forest between lowland rainforest and highland pine and oak forest. **table S2.** Freshwater insect taxa and functional feeding groups in the streams of Salinas, Polochic, and Cahabon rivers watersheds. CF = collector-filter, CF-PR = collector-filter/predator, CG = collector-gatherer, Pc = piercer, Pr = predator, Pr-Sh = predator and shredder, Sc = scrapper, and Sh = shredder.

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